

The University of Chicago

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AND LEADERSHIP IN THE
GREEN SUNFISH

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY

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SOME RELATIONS BETWEEN TERRITORY, SOCIAL HIERARCHY, AND LEADERSHIP IN THE GREEN SUNFISH (*LEPOMIS CYANELLUS*)¹

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THERE is a basic and widespread tendency for living things to aggregate, more often than not with mutual benefit (Allee, 1931). Integration of vertebrate aggregates is influenced by three major principles of behavior—territoriality, hierarchy, and leadership. Many species appear to organize in accordance with but one of these principles; nevertheless, in most instances traces of the operation of all three may eventually be recognized.

The modern concept of territory was first presented by Altum (1868) and Howard (1907-14). Although many observations have been gathered since Howard's (1920) stimulating book, few detailed studies of territorial behavior are yet available. Noble (1939a) gives a simple, inclusive definition of territory as "any defended area." Nice (1941) reviews the literature on birds and classifies a number of types of territory with regard to mating, nesting, feeding of young, roosting, etc. Territorial behavior seems to be most varied in birds but is also prevalent in the bony fishes, reptiles, and mammals.

Social hierarchies in domestic fowl were described by Schjelderup-Ebbe (1922, 1935). Small flocks of hens maintain a linear system of dominance, which has come to be called the "peck-right."

¹ This study originated from a suggestion by Dr. W. C. Allee, to whom the author is deeply indebted for friendly guidance. Dr. C. M. Breder, Karl P. Schmidt, and Clifford H. Pope read the manuscript and contributed much helpful criticism.

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The dominant bird has the right to peck all the others without, in turn, being pecked; the next in rank can attack all except the first; and so on down the line. Masure and Allee (1934a, b) confirmed the existence of this social order in chickens but found that certain other species of birds have a more flexible type of relation, which they named "peck-dominance." The dominant individual delivers more blows than it receives, but the subordinate often retaliates, and the outcome of any single contact is not strictly predictable. Masure and Allee observed that certain members of a group are more aggressive in one place than in another, and Allee (1942) suggests that this territoriality may be an underlying factor in the peck-dominance type of society.

Still other kinds of relations between territory and hierarchy have been proposed by Diebschlag (1941) for pigeons and by Greenberg and Noble (1939, 1942, 1944) for the American chameleon, *Anolis*. Diebschlag discovered that pigeons defend both residence points of limited area and "influence spheres," which may extend to an entire laboratory cage. Individuals were observed to engage in peck-dominance exchanges with others that held residence areas within the formers' spheres of influence. Greenberg and Noble recorded similar situations in *Anolis* lizard groups; however, the relations between the territory-holding males were of the peck-right type.

Leadership-followership phenomena

are well known in birds and mammals, but few thorough studies have yet been made. It is difficult to define leadership so as to exclude social facilitation, which Allee (1947) considers to be "any increment in frequency, intensity or complexity of behavior of one individual resulting from the presence of another." A common example of this effect is the consumption of more food by animals in groups than when isolated. Leadership seems to be a special case of facilitation, in which one animal sets the pace of group activity or initiates changes in it of various kinds.

An urgent problem in this area of sociology is the accumulation of data concerning the social behavior of lower vertebrates. On the well-grounded assumption that mammalian and avian behavior patterns stem from those of reptilian ancestors and that homologies can be drawn with the inheritable behavior of amphibians and fishes, it would seem to be of fundamental importance to trace the social instincts by comparisons between the vertebrate classes. It is difficult and sometimes impossible to distinguish homologous from analogous behavior, but valid generalizations of broad significance can often be discerned (Allee, 1938, 1945; Noble, 1938, 1939a, b; Collias, 1944).

Early in the present study it was discovered that small groups of immature sunfish (*Lepomis cyanellus* Raf.) establish hierarchies but may also become organized territorially. A simple kind of leadership or facilitation of behavior was noted. Therefore, it has been possible to undertake an experimental analysis of the relations between these types of social organization.

THE ANIMALS AND THEIR TREATMENT

The experiments reported here were designed to investigate (1) the types of

organization established by small groups of immature sunfish, (2) some of the factors that determine position in a hierarchy or other organization, and (3) the effects of certain formalized complications of the physical environment upon organization. In addition, control observations were made of the adult fighting and courtship patterns.

All the sunfish used in this study were collected from a small permanent pond in the Tinley Park Forest Preserve in Illinois. A wide range of sizes and probably of ages was found during the summer of 1944, and in the fall a stock was maintained in large aquaria. These fishes were used throughout the following year until early summer, when immature fishes again became abundant. Collections were made also in July and August, 1946.

Hubbs and Cooper (1935) state that green sunfish ordinarily do not reach sexual maturity until they are about 3 inches in length; they found very few of the second-summer fish to be mature. For my experiments, individuals were selected that ranged from about 0.75 to 1.5 inches in standard length. It is almost certain that none of these was more than 1 year old. Sex could not be distinguished externally but was determined later at autopsy. Individuals could be identified through the circumstance that they had encysted parasites (trematodes) imbedded in skin and muscle and, in fact, all through the body; the parasites formed distinctive patterns of black-pigmented dots. The behavior of these fishes differed in no discernible way from that of noninfested sunfish collected from Hyde Lake, Illinois. Groups were selected in which the members could be identified readily and did not vary greatly in size.

Some of the experimental aquaria were situated in the Whitman Labora-

tory greenhouse, but the greater part of the study was performed in a large laboratory room, where the aquaria were kept under fluorescent lighting. Screens were arranged so as to minimize outside disturbance. The water used was Lake Michigan tap water, either heated or run through a charcoal filter to remove the toxic chlorine; it was changed in the aquaria every 4-7 days. The fishes were fed daily with enchytraeid worms, tubifex worms, or a cooked mixture of corn and soy meal, supplemented with liver or egg yolk. They grew best on live food but also did well on the substitutes.

In the experiments involving manipulation of environmental relations, single or multiple galvanized-wire partitions were set into the aquaria, each with a 2-inch square opening at the bottom. Details of procedure in the various experiments can most conveniently be given with the results.

BEHAVIOR PATTERNS

AGGRESSIVE BEHAVIOR

Sunfish that have settled their dominance relations do not ordinarily fight in the sense of showing the full fighting pattern. Instead, the dominant individuals drive their subordinates, that is, they make quick dashes at them, and the latter swim away, usually without being nipped. Occasionally, two may threaten by spreading their gill-covers and moving head-on toward each other; the threatened individual turns broadside and, with body held rigid, vibrates in a weaving fashion. An encounter seldom goes any further, unless the two are strangers.

The full fighting pattern of the immature sunfish cannot be distinguished in any particular from that of the adults. In both there is the same remarkable set of special pigmentation. The bony opercular flap has a large black spot, mar-

gined with salmon-red on the flexible portion. When fighting, the fish spreads its gill-covers, and this gesture carries the red-margined patch of black, which roughly resembles an eye, out to a position where it appears to the observer that the head has suddenly become very much enlarged. Another concentration of black pigment is present on the flexible portion of the dorsal fin and less conspicuously also on the anal fin. These spots darken and lighten with the apparent excitation of the fish. An actively fighting individual almost always has these spots intensified, but, if it loses the fight, the spots disappear. An interesting series of changes in eye color occurs during fighting. The iris is normally lightly pigmented, with a variable amount of red around the pupil. During an encounter, the red becomes more prominent, and a dark, inverted triangle appears above the pupil. If the fish loses, black pigment spreads to the rest of the iris and the red is obscured. A "black eye" is here an unfailing sign of defeat.

During the breeding season, male green sunfish develop fringes of white on the dorsal, caudal, anal, and pelvic fins. The latter have thickened anterior rays, although this does not seem to be connected with mating behavior. All the various tints of the male are strengthened at this time. The female, on the other hand, becomes less conspicuous. Females, and also subordinate individuals of either sex, exhibit a dorsoventral striping or banding of light and dark. There is some overlap in regard to the sex-specificity of these color patterns. Immature females often show the white margining of the fins but to a lesser extent than the males, and subordinate males are somewhat banded.

The initial move in the fighting pattern consists of a head-on advance toward the opponent, with gill-covers

erected; the latter responds with a seemingly defensive measure, namely, a weaving motion that appears to help in either avoiding or mitigating the force of a blow. The fishes take turns in advancing and weaving, but soon begin to nip furiously at head or body. Often they will catch onto each other's jaws and hold until one breaks away. When the fight is lengthy, the movements tend to become formalized, and as the opponents tire, they may move side by side, making weaving motions, or alternate in threatening, weaving, and nipping.

Females show the same fighting pattern as the males except when ready to spawn, at which time they are very subordinate.

REPRODUCTIVE BEHAVIOR

During the winter and spring (1944-45) a number of sunfish grew to mature

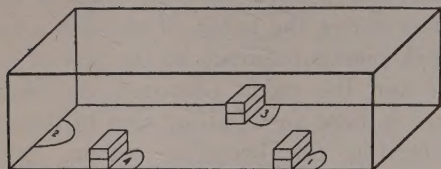


FIG. 1.—Breeding aquarium. Bricks were piled up to provide nest sites; the shorter sides of the aquarium are opaque.

size in the laboratory, and in May an attempt was made to induce them to breed. Two large aquaria ($8 \times 2 \times 1.3$ feet) were arranged for this purpose, as shown in Figure 1. The bottom was covered with about 1 inch of coarse sand, and bricks were placed at intervals, as indicated, to provide the kind of shielding barrier used by some species of sunfish (Breder, 1936).

In the first trial, two large males and what appeared to be a female were placed in one of the aquaria. After several days, a male dug an oval nest at position 1 and, sometime later, the other male nested at position 2, at the opposite end of the aquarium. On May 23, Male 1 and the female spawned at position 1, after

which the female paid no further attention to the nest, while the male continued to guard the eggs. On June 2 the female was seen on the second nest, responding to courtship but not laying any eggs. On June 6, tiny fishes were detected; the adults were immediately removed in order to rear the young. Meanwhile, the same males were placed in the second aquarium, together with two other equally large males. To make conditions more nearly like the pond environment, 7 smaller fishes were added that were about half the size of the males. The first two males that had established nests at 1 and 2 in the first aquarium repeated their performance in the closely similar habitat in corresponding places. In addition, the two new large males built nests at positions 3 and 4 (Fig. 1). The group of smaller fishes did not nest but engaged in nipping and chasing among themselves; all were strictly subordinate to the large males.

Nest 3 was the least secure, and the male on it was subject to drives by Male 1 and Male 4. The latter especially exercised dominance over Male 3 in "nip-right" fashion so that for more than a month a kind of "territorial" hierarchy (Greenberg and Noble, 1944) could be detected, with Male 3 able to defend his nest only against the smaller fishes.

There was no sizable female available, and after a time it was observed that the borders of nest 1 were being progressively enlarged, almost to the extent of destruction of the nest. Finally, on July 9, a small female was observed to spawn with Male 2; she was about half the size of the male, but the behavior of both was the same as in the mating seen earlier, and eggs were laid. Nesting behavior on the part of the males continued until the middle of August, when they began to move about more freely, with less attention to the nests.

The pattern of courtship and mating of *L. cyanellus* has not hitherto been recorded in the literature; it was very similar in all observed instances. While the male attempts to drive the female toward the nest and will make repeated excursions in her direction to do so, it is the female that determines when spawning will occur. The driving male behaves in the same manner as toward a male rival, but with much less intensity. The female finally circles the nest and comes to rest with head toward the angle made by the bricks and the glass. Here the male

the corner. At intervals, he nips her and she leaves the nest, only to return after a short time. When the female is out of the nest, the male enters the corner head-first, and makes vibratory fanning movements with his tail.

During the various experiments, the immature fishes never showed the complete courtship pattern. In a single instance, observed from July 26 to August 12, 1945, a small male behaved in a peculiar fashion on a territory, and some phases of sexual behavior were detected such as circling a particular spot, driving

TABLE 1

SUMMARY OF DATA CONCERNING 44 GROUPS OF 4 SUNFISH EACH, KEPT IN SMALL, BARE AQUARIA (10X8X8.5 INCHES) CONTAINING 4 LITERS OF WATER

	Expt. I	Expt. II	Expt. III	Expt. IV	Expt. V	Totals
Number of aquaria.....	8	8	8	8	12	44
Duration in calendar days..	19	19	25	22	22	
Number of observation days	15	17	17	15	14	
Length of observation period (in minutes).....	10	10	15	15	15	
Total recorded drives..	4,258	3,733	7,707	5,592	10,244	31,534
Av. drives per group/hour.	240*	164.6	226.6	186.4	244	214.6

* Group 5 with four territories was omitted because too few drives were recorded (62).

moves to a position directly over her. As he does so, the pair surge together into the corner, the male pressing on the back of the female; she turns ventral side up, rising upward; as her belly approaches that of the male, eggs are seen to be emitted from the genital opening. The pair move back and forth in the corner; at each movement the female presses her belly upward, close to the male's cloacal opening, and small numbers of eggs are expressed, to fall on the sides of the nest, on the plants bordering it, and in the nest itself. Sperm could not be seen, but fertilization undoubtedly occurred, since the eggs later hatched. The pair may stop and circle the nest, with the male at the outside, herding the female toward

others toward it, and moving above another fish. This was an exceptional observation.

TYPES OF SOCIAL ORGANIZATION

The first series of experiments involved forty-four groups of four sunfish each, in small, bare aquaria (10 X 8 X 8.5 inches) containing 4 liters of water. These groups were observed for 19-25 days, between October 2, 1944, and January 14, 1946 (Table 1).

In the majority of the groups (27) the fishes developed a dominance order or hierarchy. A single individual became dominant and was able to move unhindered over the whole aquarium and freely drive all the others, whereas a

second fish could drive the remaining two, and a third drove only the fourth or "omega" fish. Such relations were often established by the very first day of observation and persisted, except for temporary reversals, during most of the observation period.

In the remaining seventeen aquaria, two or more individuals defended territories. In four cases, two fishes held territory, and the others were not only subordinate to them but were also organized in a hierarchical relationship. In twelve cases, three of the four held territories, while the fourth was subordinate to all. In the one unusual case, all four mem-

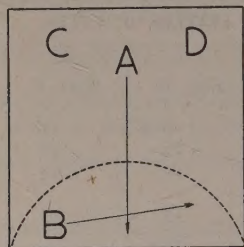


FIG. 2.—"Partial" territory. *A* is dominant in the whole aquarium, while *B* defends a small area against all but *A*.

bers of a group succeeded in holding territories; the lowest-ranking fish was the last to establish itself. Further details concerning these territories will be given below.

It was impracticable to distinguish cases of a single fish holding territory from those in which a despot ruled the entire aquarium. With a floor space of about half a square foot, the dominant fish frequently darted across the entire area to attack a subordinate. Territoriality was clear enough, however, when two fishes threatened each other, neither dominant, and subdivided the available space, although with a somewhat indefinite boundary. Perhaps all hierarchies in small laboratory aquaria should be considered as single territories

held by the despot, but the concept of territory as "any defended area" implies boundaries, defended against trespass. In the case of a single territory, therefore, it would be necessary to show that the boundaries lie within the aquarium walls, i.e., that the dominant fish voluntarily restricted its defensive reactions to only part of the total area. Presumably, in nature, boundaries are set by interaction between neighboring territory-holders, and available space is thus parceled out. Experimental conditions would seem to rule out the category of "single territory" from consideration in this series of experiments.

The twenty-seven hierarchies were complicated by "incipient" or "partial" territoriality. This was not difficult to recognize in seventeen instances; the fish ranking next to the despot was observed to take up residence in a corner or side of the aquarium and defended this area against trespass by all but the despot. The first-ranking fish could enter and drive this territory-holder, but the latter would often resist and would resume its defense when the despot left the immediate area. In the remaining ten cases this behavior was less evident and was not recorded as such.

The concept of "partial" territory differs somewhat from Diebschlag's (1941) terminology of "resting place" and "influence sphere." Figure 2 may serve to illustrate the kind of relationship observed in green sunfish. Here *A* is the despot, but the second-ranking fish, *B*, defends the area indicated by a dotted line whenever *A* does not interfere. Individuals *C* and *D* do not defend any specific place but rest more often in the indicated corners than elsewhere, and they can be said to have resting places. In this case there are no limits to the "influence sphere" or territory of *A*; the artificiality of aquarium conditions elim-

inates territory-holding neighbors and boundaries which would be delimited by mutual adjustment. Hence *A* does not hold the same kind of territory that exists when two or more fishes subdivide the aquarium space.

The partial territory of *B* may represent a step toward later equality with *A*, or it can result from a change in the status of *B*, which might previously have held full territory. In either circumstance, partial territory may be considered as intermediate between hierarchy and territory.

Even under our laboratory conditions, with oversimplification of habitat and limitations of space, territoriality is an outstanding phenomenon in the social life of immature sunfish. The territorial nesting behavior of adult male sunfish during the breeding season was known to naturalists long before its description by Reighard (1902), but there is no mention in the literature of territorial behavior in the immature fish of any species. The present experiment demonstrates that first-year green sunfish show aggressive behavior and defend territories, although not yet hormonally stimulated to exhibit reproductive behavior.

DESCRIPTION OF HIERARCHIES

Behavior on first encounter was variable, and usually the fishes spent some time becoming accustomed to the aquarium before reacting to one another. Soon one fish threatened another, eliciting either avoidance or counterthreat. Dominance was often decided by the early submission of a nonaggressive or smaller individual. If the fishes were fairly well matched, vigorous fights occurred at any time within the first hour and sometimes continued intermittently throughout the day. The winner showed the right to "drive" its subordinate, and the latter retreated. In most instances the sub-

ordinates became well trained to retreat and did so at the first move in their direction. As a result, the dominant fish seldom spread its gillcovers or showed other signs of the fighting pattern and rarely came close enough to nip. Such a "drive-order" contrasts with the "nip-order" described by Braddock (1945) for *Platy-poecilus maculatus*.

Within a few days after the establishment of the hierarchy, its members settled down to incessant aggressive activity. In twenty-six groups,³ the most dominant member drove its three subordinates at the average rate of 44.3 attacks per hour, the next-ranking individual drove its subordinates an average of 29.2 attacks per hour, the third-ranking fish drove its subordinate at a rate of 14.7 attacks per hour, and the lowest-ranking fish resisted its superiors at the average rate of 1.7 drives per hour (Table 3). In spite of this high frequency of aggressive interaction, the hierarchies were fairly stable. In seven of the above twenty-six groups, the rank order that pertained on the first day of observation remained unchanged, except for one or two temporary reversals. In another case the two upper ranks reversed after a few days and thereafter relations remained constant. A permanent upset of the two intermediate positions occurred in nine groups, whereas in four others the lowest fishes either exchanged places or never completely settled the dominance order. In four groups a single fish died and was replaced, with consequent changes in the hierarchy. In the remaining case, early instability of the three lower ranks was followed after 4 days by settling of relations.

The total drives made and received by fishes occupying each of the four ranks

³ One group (No. 6, Expt. V), has been omitted from the total figures because the rank order was reversed several times (Table 7).

are compared in Table 2. The data for each hierarchy represent the longest stable interval during the observation period, and the nature of any major changes that took place is indicated. Table 3 presents the averages for each rank in terms of drives per hour of observation; the fishes occupying the alpha, or highest, positions drove their subordinates quite equally, on the average, regardless of rank. The beta, or second-ranking, fishes showed a tendency to drive their lower-ranking subordinates more often, although this was not statistically significant. The number of drives given are directly correlated with rank, whereas the drives received are inversely correlated.

A total of 582 reverse drives (subordinate driving superior) is recorded in Table 2. The fishes in each rank category were resisted in direct proportion to the rank of the subordinate. The orderly progression of numbers shown in Tables 2 and 3 suggests that the members of a hierarchy occupy steplike levels in dominance. The most dominant fish not only drives all the others but drives more frequently; resistance to the alpha fish is also weakest, as shown by the low frequency of return drives that it receives. The second-ranking fish drives its subordinates more actively than does the third-ranking fish and is resisted more actively by the latter than by omegas or lowest-ranking fish. The third-ranking individuals, while decisively dominating the omegas, also receive a large number of drives in return.

The majority of the hierarchy relations were of the stable "peck-right" type. Table 4 presents the frequency distribution of reverse drives in each of the six contact-pair relations. In sixty-four instances, the subordinate did not return the drives of its superior, while in thirty-five other cases it did so only once or

twice. Relations between the despot fish and its three subordinates were more decisive than among the others; in the lower ranks, reciprocal driving was seen much more frequently (Table 2). In such cases one can consider the relation to be similar to the flexible "peck-dominance" of pigeons (Masure and Allee, 1934a). At any given time, either the dominant or the subordinate member of the contact-pair might be driving, with a better chance that it will be the dominant.

The stability of the relationships can also be shown by analyzing their duration in terms of percentage of total observation time. Table 5 gives the longest duration in calendar days of each of the six contact-pairs, arranging the members of the group by their rank assigned in Table 2; next to the duration is the percentage of the observation period that it represents. It may be seen that dominance was quite stable; the alpha rank was most consistently maintained, remaining unchanged for an average of 97 per cent of the observation period. In preparing this table a change was considered to have occurred whenever a subordinate drove its superior two or more times in excess of the number of times it was driven during the observation interval (10-15 minutes). Such changes were seldom permanent except during the early stages of hierarchy formation and for a few days afterward. The changes usually again were reversed in favor of the consistently dominant fish.

Table 6 presents an analysis of the duration of the entire hierarchy and of various subrelationships within it. The single pair-contacts lasted, on the average, 88 per cent of the observation period. Alpha dominated its subordinates very consistently (97 per cent of the time, on the average), whereas beta and gamma were not quite so effective (70 and 74 per cent, respectively). The hierarchy itself lasted

TABLE 2

TOTAL DRIVES GIVEN AND RECEIVED IN EACH OF THE 6 PAIR-CONTACTS
COMPRISING A HIERARCHY OF 4 MEMBERS

GROUP NUMBER	PAIR-RELATIONS						DAYS DURA- TION	TYPE OF CHANGE*
	A—B	A—C	A—D	B—C	B—D	C—D		
Experiment I								
I.....	79— I	69— 0	49— 0	35— I	17— 2	6— 2	9	c
3.....	46— I	128— 0	233— 0	61— 2	150— 4	60— I	19	a
4.....	111— I	96— 0	97— 0	46— I	92— 6	12— 3	15	c
6.....	87— 2	185— 0	130— 0	41— 5	87— I	50— 10	19	a
7.....	82— 0	187— 0	163— 0	49— II	88— 9	34— 12	12	c
8.....	36— 3	79— 0	75— 0	139— 0	191— 0	9— 0	19	a
Experiment II								
17.....	41— 2	32— 0	30— 0	59— 37	52— 12	30— 4	10	c
20.....	71— 5	81— I	99— 0	53— II	42— 16	21— 14	15	c
21.....	64— 6	44— 3	40— 4	52— 2	47— 2	7— I	9	b
22.....	45— 10	26— 0	62— I	38— II	37— 4	11— 2	10	c
23.....	71— 0	111— 0	59— 0	10— 7	23— 3	25— 8	14	e
24.....	32— 5	18— I	30— 0	43— I	111— I	6— 4	19	d
Experiment III								
6.....	187— 0	96— 0	11— 0	43— 10	23— 6	56— 9	16	c
12.....	364— 2	231— 0	199— 0	137— 18	223— I	169— 11	25	a
15.....	121— 6	206— 3	226— 0	77— 4	83— 8	43— 15	25	a
18.....	237— 6	99— 0	198— 3	105— 6	109— 34	33— 16	25	a
Experiment IV								
3.....	172— 0	141— 0	96— 0	27— 5	29— 7	23— 22	19	d
15.....	63— 0	54— I	62— 0	34— 3	43— 0	80— 0	8	c
Experiment V								
5.....	139— 10	93— I	64— 0	129— 7	117— 0	26— 0	16	f
7.....	173— 0	167— 0	106— 0	19— 11	41— I	33— 18	17	d, f
8.....	178— 0	157— 0	118— 0	54— 9	35— 2	9— 2	22	a
18.....	97— 0	89— 0	59— 0	37— 0	14— 9	35— 3	21	d
19.....	90— I	145— 0	135— I	41— 12	31— 6	37— 15	15	f
20.....	154— 0	89— 0	176— 0	23— 5	37— 4	14— 8	15	c
25.....	117— 0	150— I	135— 0	118— 2	122— 0	104— 2	15	d
26.....	126— 0	90— 0	87— 0	91— 0	120— 0	17— 0	11	f
Totals..	2,983— 61	2,863— 11	2,739— 9	1,561— 181	1,964— 138	950— 182		

* a, No permanent changes in hierarchy; b, A—B pair-contact reversed permanently; c, B—C pair-contact reversed permanently; d, C—D pair-contact reversed or unsettled; e, early instability of lower three ranks, stable after 4 days; f, one fish died and was replaced, leading to changes in the hierarchy.

unchanged for an average of 54 per cent of the observation period.

In general, the hierarchies appeared to become more stable with time. There were some exceptions, in which permanent reversal of ranks occurred well along in the observations. In one case (Group 6, Expt. V), the fish ranking third at the start worked its way up to first and, in the process, brought about a series of changes in the hierarchy, as shown in Table 7. As L rose in rank, M dropped to omega. There was a parallel

rise in rank of N to second place, and, as a result, O dropped to a fairly consistent third. All these fishes were females, and they were very closely matched in size at the start. At the end of the experiment, however, it was found that L and N had grown considerably more than M and O, so that a decided size discrepancy resulted.

This introduces the whole matter of position in the social hierarchy and growth, a subject that is reserved for a joint communication later with others

TABLE 3
AVERAGE RATES OF DRIVING PER HOUR OF OBSERVATION
IN 26 HIERARCHIES OF FOUR MEMBERS

RANK OF DRIVING FISH	RANK OF FISH DRIVEN			
	A	B	C	D
A.....		44.6±2.4	44.1±1.4	44.1±3.9
B.....	0.97±0.23		26.8±2.9	31.5±3.7
C.....	0.19±0.08	3.3±1.0		14.7±2.1
D.....	0.15±0.09	2.2±0.5	2.7±1.1	

TABLE 4
FREQUENCY DISTRIBUTION OF NUMBER OF REVERSE DRIVES IN EACH
OF THE 6 CONTACT-PAIRS OF 26 HIERARCHIES
(Pair-Relations Are in Order of Rank)

NUMBER OF BACK-DRIVES	FREQUENCY OF OCCURRENCE						TOTAL
	A—B	A—C	A—D	B—C	B—D	C—D	
0.....	11	19	22	3	5	4	64
1.....	4	5	2	3	4	2	20
2.....	3	0	1	3	4	4	15
3.....	1	2	1	1	1	2	8
4.....	0	0	0	1	3	2	6
5.....	2	0	0	3	0	0	5
6.....	3	0	0	1	3	0	7
7.....	0	0	0	2	1	0	3
8.....	0	0	0	0	1	2	3
9.....	0	0	0	1	2	1	4
10.....	2	0	0	1	0	1	4
11.....	0	0	0	4	0	1	5
12.....	0	0	0	1	0	1	2
Over 12.....	0	0	0	2	2	6	10
Total pair-con- tacts.....	26	26	26	26	26	26	156

TABLE 5

LONGEST DURATION OF THE PAIR-CONTACTS IN 26 HIERARCHIES
(Expressed in Calendar Days and Percentage of Total Observation Period)

GROUP No.	A—B		A—C		A—D		B—C		B—D		C—D	
	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent
Experiment I												
I.....	19	100	19	100	19	100	7	37	19	100	19	100
3.....	19	100	19	100	19	100	19	100	19	100	19	100
4.....	19	100	19	100	19	100	15	79	12	63	9	47
6.....	19	100	19	100	19	100	19	100	19	100	10	53
7.....	19	100	19	100	19	100	9	47	11	58	11	58
8.....	13	68	19	100	19	100	19	100	19	100	19	100
Experiment II												
17.....	19	100	17	89	19	100	9	47	10	53	19	100
20.....	19	100	19	100	19	100	15	79	9	47	9	47
21.....	17	89	19	100	19	100	18	95	15	79	11	58
22.....	9	47	19	100	19	100	9	47	10	53	9	47
23.....	19	100	19	100	19	100	15	79	12	63	15	79
24.....	9	47	19	100	19	100	19	100	19	100	14	74
Experiment III												
6.....	25	100	25	100	25	100	9	36	15	60	25	100
12.....	25	100	25	100	25	100	11	44	25	100	25	100
15.....	25	100	25	100	25	100	25	100	25	100	18	72
18.....	21	84	25	100	25	100	25	100	10	40	9	36
Experiment IV												
3.....	22	100	22	100	22	100	22	100	22	100	10	45
15.....	22	100	22	100	22	100	8	36	22	100	22	100
Experiment V												
5.....	14*	100	14*	100	14*	100	14	64	22	100	22	100
7.....	22	100	17*	100	22	100	11*	65	22	100	5*	30
8.....	22	100	22	100	22	100	22	100	22	100	22	100
18.....	22	100	22	100	22	100	22	100	16	73	19	87
19.....	22	100	22	100	16*	100	22	100	13*	59	13*	59
20.....	22	100	16	73	22	100	22	100	22	100	15	68
25.....	22	100	22	100	22	100	22	100	22	100	16	73
26.....	22	100	22	100	13*	100	22	100	13*	100	13*	100
Average duration in percentage..	94		98.5		100		79		83		74	

* One member of group died.

who have been and are associated in this particular phase of the inquiry. Although the evidence is by no means sufficiently collected to allow a definitive statement, it is known that size is an important factor in determining social dominance in the green sunfish.

In connection with joint experiments on growth, a test was made to secure further evidence on the stability of these fish hierarchies. Eight groups were maintained without observation of their behavior for 33 days (March 23-May 4, 1945). After this period, the fishes in each aquarium were watched for nine daily

observation periods, each lasting 10 minutes. Tables 8 and 9 give analyses of the drives recorded and the duration of the contact-pair relationships. Relatively few reverse drives were seen and most of the contact-pairs remained unchanged throughout the 10-day period.

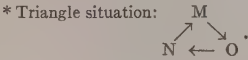
The general picture of activity within the sunfish hierarchy is fairly clear. After a time, relations tend to become formalized. The alpha fish, if its subordinates are all unaggressive, will drive at random any fish it comes across, and the omega member of the group simply avoids the approach of any of the others.

TABLE 6
DURATION OF THE 26 HIERARCHIES AND OF VARIOUS
INTERNAL SUBRELATIONSHIPS

Duration of Observation Period (Per Cent)	One Fish Dominates One Other	Alpha Dominates Three Others	Beta Dominates the Two Others	Gamma Dominates Delta	Four Fishes Maintain Same Hierarchy
I- 10.....	0	0	0	0	0
11- 20.....	0	0	0	0	0
21- 30.....	1	0	1	1	3
31- 40.....	4	0	3	1	4
41- 50.....	11	2	4	3	5
51- 60.....	10	0	5	5	6
61- 70.....	5	1	2	1	3
71- 80.....	10	1	1	4	2
81- 90.....	5	2	0	1	0
91-100.....	110	20	10	10	3
Total cases.....	156	26	26	26	26
Average duration in percentage.....	88.1	97	70	74	54

TABLE 7
DAILY RANK ORDER IN A HIERARCHY WHICH SHOWED SEVERAL REVERSALS

Rank	1/14	1/16	1/19	1/20	1/21	1/24	1/25	1/27	1/28	1/29	1/31	2/2	2/3	2/4
1.....	M	M	M	M	L	L	L	L	L	L	L	L	L	L
2.....	O	O	O	L	O	N	N	*	†	N	N	N	N	O
3.....	L-N	L	L	O	N	O	O	*	†	O	M	O	O	N
4.....	L-N	N	N	N	M	M	M	*	†	M	O	M	M	M



† Only one contact seen (N drove O once).

If the second-ranking fish happens to be active and aggressive, it may be as much or more of a tyrant than its superior. It then begins to approach equality with the latter, which may drive it infrequently.

Conditioning up and down the scale has been observed within the hierarchy. Frequently, a second- or third-ranking fish, after repeatedly driving a subordi-

nate, may then challenge a superior, usually with disastrous results. Conversely, repeated attacks by alpha may weaken the resistance of beta or gamma to drives by the others, leading to temporary changes in position.

An interesting example of conditioning is the phenomenon here called the "substitution" effect. In several cases the lowest-ranking fish was observed to take

TABLE 8

TOTAL DRIVES RECORDED IN EACH OF THE PAIR-RELATIONS OF 8 HIERARCHIES
MAINTAINED FOR 43 CALENDAR DAYS AND OBSERVED ONLY
DURING LAST 10 CALENDAR DAYS (EXPT. VI)

GROUP NO.	PAIR-RELATIONS IN ORDER OF RANK					
	A-B	A-C	A-D	B-C	B-D	C-D
1.....	78-1	49-0	36-0	29-13	28-2	62-4
2.....	56-1	63-0	74-0	64-3	108-0	31-0
3.....	44-0	83-0	62-0	10-14	18-0	91-1
4.....	38-1	46-0	37-0	21-6	70-0	33-0
5.....	113-3	72-0	47-0	34-0	24-0	2-1
6*	14-0	89-0	68-0	54-0	45-0	13-4
7.....	75-0	70-0	77-0	49-0	46-3	9-4
8.....	10-2	45-10	32-0	4-3	6-0	8-0
Totals.....	428-8	517-10	433-0	265-39	345-5	249-14

* Two territories, held by A and B.

TABLE 9

LONGEST DURATION OF PAIR-RELATIONS IN HIERARCHIES OF TABLE 8

GROUP NO.	A-B		A-C		A-D		B-C		B-D		C-D	
	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent	Days	Per Cent
1.....	10	100	10	100	10	100	3	30	10	100	10	100
2.....	10	100	10	100	10	100	10	100	10	100	10	100
3.....	10	100	10	100	10	100	4	40	10	100	10	100
4.....	10	100	10	100	10	100	9	90	10	100	10	100
5.....	10	100	10	100	10	100	10	100	10	100	10	100
6*	10	100	10	100	10	100	10	100	10	100	5	50
7.....	10	100	10	100	10	100	10	100	10	100	9	90
8.....	10	100	10	100	10	100	10	100	10	100	10	100
Average duration in percentage	100		100		100		82.5		100		92.5	

* Two territories, held by A and B.

advantage of the tendency of beta and gamma to flee the approach of the despot; it would dash at them, and they would run, unless they turned around to fight back, and then they would drive omega away with ease. Some of the reverse drives recorded in Table 2 undoubtedly can be traced to this kind of substitution, which also was performed by the others.

FACTORS IN DOMINANCE

Among the factors that can be postulated as affecting the outcome of a fight or the place of an individual in a rank order, sex, size, and previous experience or conditioning lend themselves most readily to experimentation. Although the sex of the immature fish could not be told externally, it was possible to distinguish the sex composition of the groups at autopsy by macroscopic inspection of the gonads (method checked by cross-section of gonads). In Experiments II-V, distribution of the sexes was determined and found to be 78 males to 66 females. Additional data on the effect of sex on hierarchy position were also secured from Experiment VI and from two other sets of ten groups each, observed under the same conditions as the others, but for a shorter time—August 6–August 10 and August 29–September 6. These two sets were controls for an experiment on the effect of screen partitions on the form of social organization (to be reported below). From these eight sets of experiments, totaling seventy-two groups, sixteen can be selected that fulfil the following conditions: first, they were hierarchies, not complicated by established territory; and, second, they consisted of two males and two females. In these sixteen critical cases, the alpha rank was held by fourteen males and two females, the beta rank by eleven males and five

females, the gamma rank was held by four males and twelve females, and the omega or lowest rank by three males and thirteen females. This indicates a correlation between maleness and high social rank.

During the early stages of formation of a hierarchy, the relative size of the fish is an important factor. Large sunfish dominate much smaller individuals without resistance by the latter; even within the minor range of size differences that were present, the larger fishes regularly occupied the higher ranks. Since both sex and size are factors in dominance, the question arises as to how they interact. To what extent does larger size overcome the handicap of femaleness? Some indication can be secured by re-examining the sixteen cases already discussed as critical for the sex factor. There are ninety-six pair-relations represented, of which two-thirds are heterosexual and a third unisexual. In sixteen male-male contact-pairs, the dominant individual was the larger in eleven cases; the dominant female was the larger in nine of the sixteen female-female pair-contacts. In sixty-four heterosexual contacts, the dominant male was larger in forty-four of fifty-three cases, while the dominant female was larger in seven of eleven cases. The fact that so many of the males that dominated females were also larger somewhat confuses the picture. It is possible, although not probable, that this may be a systematic error arising from the composition of the field collections. Hubbs and Cooper (1935) found that male sunfish in nature grow faster than females but are not significantly larger until their third summer. Our laboratory experiments made in another connection demonstrate a significantly faster rate of growth of males over females in the first and second years.

Hubbs and Cooper suggest that "the

increased growth of the males has been of selectional significance, enabling them to ward off enemies from the nests which they guard so pugnaciously." This hypothesis may be restated by defining enemies to include intra-specific male rivals; and the selection would then be in part also intra-specific sexual selection of the Darwinian type (Huxley, 1938).

The effect of conditioning on the members of a hierarchy has already been mentioned. The members of a group develop stereotyped reactions to one another and to the aquarium; place conditioning is especially prominent and may lead to territory; but, even when no definite territories exist, each fish tends to stay more often in a particular place than in others. The subordinates have certain positions in which they are safer from attack than elsewhere and also develop movement habits that take them out of the path of their superiors in rank.

When a new fish is introduced to replace a member of the group, it is quickly relegated to the bottom rank, unless it is much larger. The newcomer transgresses upon all the relations that have developed and at first is driven by each resident fish. After a while, however, the newcomer begins to assert itself and may advance in rank. Thus, in Group 5, Experiment V, a fish introduced as replacement for the omega rose to the alpha position in a few days.

From May 9 to May 11, 1945, the dominant individuals in the hierarchy groups of Experiment VI were interchanged to see what rank a long-established alpha fish would take in a strange hierarchy. The alphas that were exchanged differed in size by little more than 1 mm. in three instances but were somewhat unequal in the fourth case. Since these individuals were long accustomed to be dominant, it was of interest to see whether they could substitute

mechanically for each other or whether they would meet with resistance.

After the exchange of the dominant fish in Groups 1 and 2, both were observed together for $1\frac{1}{2}$ hours. For the first 15 minutes, the second-ranking fish in Group 2 took over, and the newcomer went to the bottom of the hierarchy; soon, however, it began to return challenges and within another 20 minutes it had succeeded in defeating all the resident fish and became the despot. In the other aquarium the newly introduced fish at first made persistent efforts to get through the glass of the aquarium. During this time, it was repeatedly driven by the second-ranking fish and occasionally by the others. After a while it began to resist attack, first defeating the second-ranking fish and then dominating the group.

In the second exchange, between Groups 3 and 4, events proceeded in a much similar fashion. The alphas, when placed in strange aquaria, at first did not resist attack and were driven by the residents. Within 45 minutes, however, each had won to the top.

The alpha fishes of Groups 5 and 6 were unequal in size, measuring 47.3 and 39.7 mm., respectively. When they were interchanged, the smaller went to the bottom of the new hierarchy and stayed there for 2 hours and 15 minutes of observation. In the other group the large newcomer was not active, and, although he was driven a few times and later drove once in return, no conclusive results were secured.

In the fourth exchange the two alphas were of about the same size. After 11 minutes one of them was dominant in its new group; by 31 minutes, the other had asserted itself and had become dominant. Neither encountered much opposition.

Thus in three cases the dominant fishes of two groups were exchanged and

replaced each other, rising to top rank in 35, 51, 45, 45, 11, and 31 minutes. In the remaining case one of the alphas was too small for its new group, becoming omega, and the other was unaggressive in the new situation. All these fishes, when returned to their old places, almost immediately resumed their original positions. During their absence fights occurred among the subordinates, but there were no reversals in rank.

This apparent ability of a long-dominant fish to retain its dominance even in a strange group probably resulted as much from the conditioning of the sub-

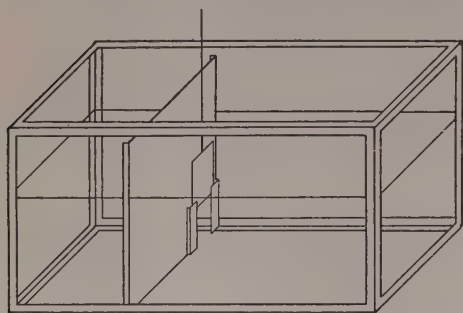


FIG. 3.—Maze used in tests of relations between leadership and hierarchy. Adapted from Welty (1934). Aquarium measures 16×10×10 inches.

ordinates as from its own previous experience. These tests are too few to be taken as approaching conclusive results, but they do indicate the importance of the factor of experience or conditioning.

HIERARCHY AND GROUP LEADERSHIP

Although the green sunfish does not school as compactly as certain other species, there are some indications of mass facilitation of activity. The fishes tend to follow one another for variable distances, and any quick movement of one fish attracts the others toward it. A fish performing a "scratch reflex" (scraping the sides of the body against any suitable object, an action that is frequently repeated) is often followed for a

short distance. The first to see food darts forward and is immediately followed. A bit of inedible material resembling food, when mouthed and spit out by one fish, is then in turn mouthed by other individuals. A subordinate driven by one territory-holding fish is then very often set upon by the adjacent territory-holder, even from some distance. Similarly, an attack on a subordinate by one of its superiors tends to draw upon it attacks by the others.

Among those vertebrate groups in which hierarchy is important, the dominant individual may be the leader, or may not, as in chickens (Fischel, 1927). From a comparative point of view, it is of considerable interest to know whether any relation between dominance and leadership prevails in teleost fishes. A simple test was designed, based on the learning experiments performed by Welty (1934) with goldfish. Six aquaria (16×10×10 inches) were arranged on a water table, the broad side toward the observer, and a wire-screen partition with gate was set about a third of the way to one side (Fig. 3). The gate was closed by a sliding door, opened from behind a burlap screen by means of a pulley. As part of the conditioning stimulus complex, a 7-watt electric bulb, set into a small shielding box, was placed in front of the larger compartment of the aquarium. On June 16, four fishes were introduced into the large compartment of each aquarium and were observed at intervals until June 19, when all the groups had become organized as hierarchies.

A trial consisted of first turning on the light and then opening the door as gently as possible, when all the fish were about an equal distance from the gate. As soon as a fish came through into the small compartment, it was fed by dropping enchytraeid worms into the water. The

following data were recorded: (1) whether the alpha fish "led" through the maze, (2) the learning time of the first fish through the maze, and (3) the time of the slowest fish at each trial.

As shown in Table 10, the dominant fish led in 47 per cent of the trials; this is about twice the frequency expected by

chance. It led more often in the first three trials (first in eleven of eighteen cases) than in the last seven trials (first in seventeen of forty-two cases). After the early trials it became a race and somewhat a matter of chance which fish reached the door first, and the dominant fish was handicapped because the observer opened the door when alpha was in the middle of the group, in neither a

position favored nor a back position. As a result, the subordinate nearest the partition had a shorter distance to travel and often darted through as soon as the door was opened.

The stimuli of turning on the light and opening the gate were separated by a brief interval, usually less than 30 sec-

TABLE 10
LEARNING TIMES (IN SECONDS) OF THE FIRST AND LAST FISH
IN GROUPS OF 4 IN WELTY-TYPE MAZE

TRIALS	GROUPS					
	1	2	3	4	5	6
1.....	{ 370* 405	{ 125* 285	{ 140 170	{ 160 405	{ 120 395	{ 60* 75
2.....	{ 130 140	{ 80* 105	{ 55* 65	{ 50 85	{ 10* 20	{ 10 25
3.....	{ 30 45	{ 30* 35	{ 60* 65	{ 10* 20	{ 10 15	{ 10* 30
4.....	{ 15 30	{ 5 20	{ 30 35	{ 5 20	{ 10* 20	{ 10* 15
5.....	{ 2 10	{ 5* 10	{ 2 20	{ 1 5	{ 10* 15	{ 5 10
6.....	{ 2* 5	{ 2* 5	{ 5* 10	{ 2* 20	{ 10* 20	{ 2* 5
7.....	{ 2* 5	{ 15 75	{ 2* 15	{ 1 5	{ 2 4	{ 2 4
8.....	{ 1* 30	{ 1 10	{ 1 5	{ 1 5	{ 1 2	{ 5 40
9.....	{ 1 3	{ 1 15	{ 1 2	{ 2 10	{ 1 2	{ 1* 2
10.....	{ 1 10	{ 1* 2	{ 2* 30	{ 1* 2	{ 1* 3	{ 2 5

* The dominant fish in the group came through gate first.

chance. It led more often in the first three trials (first in eleven of eighteen cases) than in the last seven trials (first in seventeen of forty-two cases). After the early trials it became a race and somewhat a matter of chance which fish reached the door first, and the dominant fish was handicapped because the observer opened the door when alpha was in the middle of the group, in neither a

position favored nor a back position. As a result, the subordinate nearest the partition had a shorter distance to travel and often darted through as soon as the door was opened.

As seen in Table 10, the learning time

dropped steeply at the second and third trials. These are not the records of individual fishes but of the fastest and slowest through the maze at each trial. An important element in bringing the slower members of the group through the maze was the feeding activity and visual stimulus of the food. In the early trials a slow fish sometimes stopped at the partition near the food, finding the door by moving along the screen. After the first three trials, however, the members of the

dropping enchytraeid worms near the doorway. Table 11 presents the learning times in seven trials. Six individuals exhibited regular learning curves; two (Nos. 3 and 11) improved markedly after the fourth trial, and four (Nos. 1, 2, 4, and 12) gave irregular performances. Much of the "learning" shown by the sunfish seemed to be the overcoming of negative reactions to elements in the stimulus situation. The light, movements of the door, and vibrations in the

TABLE 11
LEARNING TIMES (IN SECONDS) OF 12 ISOLATED
SUNFISH IN WELTY-TYPE MAZE

ISOLATES	TRIALS						
	1	2	3	4	5	6	7
1.....	1,200	298	350	666	426	232	1,187
2.....	1,200	1,175	305	1,200	430	344	1,200
3.....	590	120	729	700	67	7	11
4.....	379	75	235	385	54	169	212
5.....	653	617	249	22	54	26	20
6.....	1,167	178	144	6	22	3	2
7.....	1,200	761	38	9	48	5	12
8.....	1,200	100	58	13	5	12	10
9.....	426	1,095	123	23	24	40	12
10.....	745	86	122	14	25	7	10
11.....	170	196	204	168	7	18	18
12.....	1,200	185	570	83	512	286	12

group usually came through so closely together that they fed at the same time.

Welty (1934) found that grouped goldfish learned more rapidly than did isolated ones. His work on this point has not received the experimental repetition⁴ that its importance justifies; so we tried isolated sunfish in the same maze situation as a check on the speed of learning. Twelve sunfish were placed in separate mazes and tested for learning in the same fashion as the groups were. An interval of 20 minutes was allowed for the fish to come through the gate and be fed. After that time they were lured through by

water tended to startle the isolated fishes more than they did the grouped ones. At any rate, the performance of the grouped fishes was decidedly superior to that of the isolated ones (Fig. 4).

The bearing of these facts on the problem of the relation between dominance and leadership is not wholly clear. There is group facilitation of learning, which may result from imitation, leadership-followership, or the greater "freedom from fear" afforded by group membership. Under our aquarium conditions the dominant fish tended to "lead" through the maze, at least in the early trials, which are most significant for learning. It is not clear whether this superiority

⁴Except for unpublished reports from students in Dr. Allee's classes in animal behavior.

reflects superior innate learning ability. In the early trials the dominant fish tended to explore the door and smaller compartment before the others. The dominant member of a group moves more freely in an aquarium, and this may explain in part the alert behavior of the dominant in a learning situation.

DESCRIPTION OF TERRITORIES

Seventeen of the forty-four groups comprising Experiments I-V (Table 1) became organized along territorial lines. In nine of these seventeen groups, some or all of the areas were claimed before the start of observation. A detailed record of the manner of organization of territories was secured in two cases (Groups 27 and 28, Experiment V), and a less complete account can be given of six others. The history of certain of these groups is presented in some detail because it provides an insight into the nature of territoriality.

The four members of Group 28 engaged in round-robin fights, B defeating D, and C dominating A. Soon B emerged as the despot by winning an encounter with C, the latter retaining the ability to drive A. Next, C was observed in a corner of the aquarium, which it defended against all except the despot, B. This behavior has already been defined as partial territory (p. 272). A half-hour passed, with no discernible change, and then B and D again fought; neither could dominate, but D tended to withdraw to one corner, while B remained at the opposite side (Fig. 5). Then there occurred a change in dominance between A and C; the former defeated C and took its place in the corner. After a while B challenged A, and they fought vigorously; but neither seemed to give way, and A retained its corner position. A and D challenged each other repeatedly and several times exchanged nips, neither

achieving mastery. Soon it became clear that three territories existed in the aquarium and that C was omega or subordinate to all.

An interesting change was seen the following day. The three territories still remained, but D had become the most aggressive, with the largest territory at one side of the aquarium (Fig. 6), while A and B had shifted so that they occu-

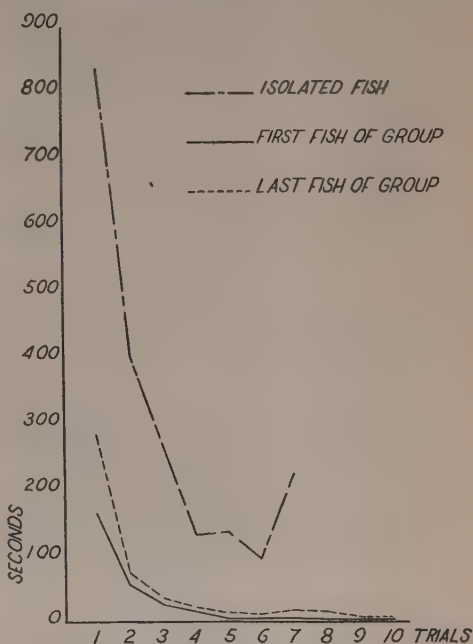


FIG. 4.—Average learning curves of isolated and grouped fishes in maze shown in Fig. 3.

pied adjacent corners opposite D. These positions were kept for the rest of the 22 days of observation. The later history of this group is discussed in part in another section (p. 288). Fish A was the least aggressive of the territory-holders, and, as a result, C was repeatedly driven into A's territory and tended to find an insecure resting place there. Thus A drove the omega actually more often than did the other fishes; nevertheless, by January 24, C was resting mainly in A's territory when exhausted, and D often in-

vaded that area to attack omega. A few days later, it was seen that D's habit of invading had worked to the detriment of A, since D now also drove A; A and B were still in territorial relation to each other at the time. On February 2, A was also driven by B whenever forced into B's area. The omega died on February 4 and thereafter A was, in effect, the lowest-ranking member of the group.

At first, Group 27 followed a similar course. Individuals C and D fought very actively soon after they were placed to-

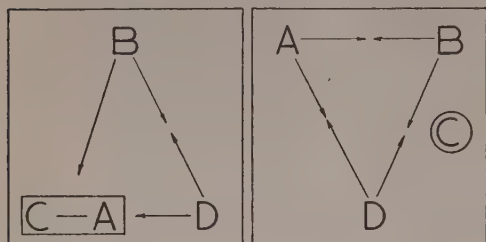


FIG. 5

FIG. 6

FIGS. 5 and 6.—Changes in territories of Group 28 (Expt. V). *B* and *D* were first to establish a mutual, territorial relation; then *A* established itself in the lower left-hand corner (Fig. 5). Next *D* became more aggressive than the others and caused a shift of the territories, as shown in Fig. 6. Apposed arrows show territory; unapposed arrows indicate dominance. *C* became omega (encircled).

gether, and *C* was the winner. In turn, *C* defeated *A* and *B* and became the despot, in control of a large part of the aquarium. Next, *B* withdrew to a corner and defended it against the others. This corner was directly opposite the usual residence of *C*, and it appeared that the location of this territory was determined by the prior position of the despot. The following day, *D* had displaced *B* and thereafter held the corner territory.

Subsequently, the two territory-holders became very aggressive and kept *A* and *B* in one corner; they remained there until January 26, when an abrupt change took place: *A* drove *B* out of the corner, chasing it persistently (forty-nine times in

15 minutes); *A* was relatively unmolested (5 drives). Thereafter, *A* gradually won a small territory in the corner; on the other hand, *B* was driven relentlessly, and on February 6 it was dead.

The sequence of events is similar in these two cases. First, vigorous fights resulted in an unstable dominance order. The resting place occupied by the most dominant individual seemed to determine an opposite pole, at which several fish alternated, and ultimately one established territory there. When the third territory was seen, it was at an intermediate position.

Seven other groups were observed initially when they still were hierarchies; in five of these, territory was eventually taken up strictly in accordance with rank in the hierarchy. The beta individual became equal in rank with the alpha, and the two restricted their movements to separate areas. When a third territory also was held (in five of the total of eight groups), the gamma fish occupied it. In one exception the two highest members of the hierarchy first held territories; 9 days later, there occurred a reversal in rank of the two subordinates, and very soon thereafter the winner also took up a territory. Another exception arose when the lowest-ranking member of a hierarchy died and the new fish that replaced it succeeded in maintaining an area against the residents. The original alpha and the newcomer both drove the other two fishes, but not each other, and stayed in separate parts of the aquarium.

This behavior of a replacing fish was seen in two other instances. In Group 9 (Experiment III), *B* and *D* were first observed to hold territories, and *C* was omega. The next day, *C* was dead and was replaced with a fish that was 4 mm. larger than *A* and $\frac{1}{2}$ mm. larger than *B* and *D*. That same day the newcomer was driven by both territory-holders but

not by A; the following day, the newcomer had become equal in rank with D, and 3 days later it held a territory alongside B and D. On the days immediately before the new fish acquired its territory, it drove omega twenty-eight and twenty-three times in two 15 minute observation intervals, chasing it into the paths of B and D, which, in turn, drove it repeatedly. It was my impression that in this manner the nonresident fish was building up an immunity from attack.

A comparable set of observations was made with Group 3 (Experiment III). At the very first observation, three territories were seen, with D as omega. Two weeks later, B lost its position and at the same time became subordinate to D. On that day, B was driven a total of one hundred and three times in 15 minutes of observation; it was dead the next day. The fish replacing B was the same size as the residents. It was attacked persistently by all, and evidently could not find a resting place in the aquarium. It was not reactive to the social relations that already existed, for example, the invisible boundaries and neutral areas, whereas D, also subject to attack, could retire to a certain corner and be safe for a while. The new fish was driven almost constantly by A and C, while D remained unmolested and even took part. On the following day, however, the newcomer had ousted D from its resting place in the former territory of B and was in process of taking over this area. Again, it was seen that in the short observation periods on consecutive days the newcomer drove omega twenty-six, twenty-nine, and seventeen times, seeming to force D out in front of it and thereby gaining a measure of immunity from attack. It held this territory until the end of observation, 5 days later.

Group 5 (Experiment I) was found to be organized into three territories at the

start of observation; A, B, and D each stayed in a corner of the aquarium and sallied out to drive C or to challenge each other. Fish C found a resting place only in the remaining unoccupied corner. Three days later, C had succeeded in repulsing drives by first A and then B, on each side of it. From then on, the four fish were all equal. They challenged but seldom drove each other, except when one trespassed on another's territory. Each stayed close to its corner and activity tended to be at a minimum, compared with other groups.

By way of summary, the following three generalizations can be made:

1. Territories may be established at any time during the course of a hierarchy and are usually taken up in order of rank. When low-ranking individuals establish territories, they first defeat their immediate subordinates.

2. Territories are, in large measure, determined by the shape of the aquarium, i.e., the corners of a square aquarium are much used as resting places. A second territory is set up at the opposite pole from an already existing one, the third is equidistant from the two others, and the rare fourth territory is located in a neutral area with relation to the three others.

3. Territories are stable but may undergo changes such as elimination of one, transfer of ownership, shifts in position and boundaries, and variations in relative aggressiveness of the possessors.

In the foregoing accounts there is a suggestion of an important social function of the omega fish. Especially in the case of territories, the omega seems to be a sort of buffer, releasing tension between the high-ranking individuals. When a territory was about to be taken, attacks upon the omega may have been an effective part of the readjustment of the group.

This suggested role of the omega was

investigated in the following series of tests. At the end of Experiment IV (December 25), Groups 18 and 21 were retained because there were three firmly held territories in each. On January 1 the omegas were removed permanently, to see whether this would affect the territories; the groups were observed for 15 minutes immediately afterward. The territories were not disrupted, but there was a rise in the frequency of challenges. On the last day of previous observation (December 25) sixteen challenges were recorded in Group 18; after the removal of omega, there were twenty-seven. In Group 21 there were three challenges on December 25 and twenty-six after the removal of omega. The omegas were kept out of the aquaria overnight, and on the following day the two groups were again observed for 15 minutes each. In Group 18 there were twenty-five challenges, four full fights, and two drives, and in Group 21 there were thirty-eight challenges and five drives.

A new fish was introduced into each group, and it was observed for 15 minutes, after a 2-minute interval for adjustment to disturbance. There were eight challenges and four drives among the three resident members of Group 18, whereas they combined to drive the nonresident fish one hundred and fifty-seven times. In Group 21 the newcomer was driven two hundred and twenty-five times in 15 minutes, keeping the residents so busy that they challenged each other only six times and drove each other seven times, occasionally perhaps by error.

These tests show that either the omega or the nonresident fish draws upon itself the attacks of the territory-holding animals and thereby reduces tension between them. In the absence of other objects of attack, fishes that have territories close together, as in our aquaria,

challenge each other, and tension may increase.

A further test was made with Groups 27 and 28 of Experiment VI. On February 4, the last day of that experiment, the omega of Group 28 died, and A, which earlier had held a territory but was now subordinate to D, came in for more than its usual share of attacks. Two days later, Group 28 was observed for 15 minutes, and during this time A was driven thirty-six times by B and eighty-two times by D. There were also eleven challenges between B and D. A new fish that had been isolated was added. The newcomer was in the same size range as the other three fishes. The group was observed for 30 minutes; during the first 15 minutes, D drove A only nine times, and B drove A just once, while B and D challenged each other six times. This was a considerable advance for A and a reduction in reactions between B and D. The latter drove the newcomer thirty-nine times, and B drove it thirteen times. The nonresident fish was forced to stay in the same corner with A, where it was driven least by B and D. In the next 15 minutes, A drove the newcomer twenty-one times and also vigorously resisted D, challenging it six times and once engaging in an active, though losing, encounter with both D and B. D drove A thirteen times, and B drove it once. There was no tension in the form of challenging between B and D. The new omega was driven ninety-six times by D and twenty-three times by B.

The omega was left in the aquarium for 24 hours, and the group was observed again for 15 minutes. The situation had improved even more for A, and it had won back its territory. It was driven only once by D and twice by B. The omega was driven thirty-three times by A, nineteen times by B, and fifty-eight times by

D. It appeared to the observer that A was driving the newcomer out in front and that it became a buffer between A and the aggressive D. Often, when D drove omega near to A, the latter, in turn, drove it out toward D's territory, and D's attention was taken up with omega, leaving A unmolested. The results, as described, indicate an important social function of the omega fish, in territorial organizations at any rate.

On February 6 the situation in Group 27 was similar to that described for Group 28; the omega had just died, and when the group was observed for 15 minutes, A was found to be the subordinate. Another fish (B') of about the same size was added; it had been kept isolated (in an adjacent aquarium). The newcomer was immediately attacked by D, but it resisted vigorously; the two were equally matched, and after 8 minutes they separated, both exhausted. The new fish drifted near A, and the latter challenged and attacked it. B' fought back and won, driving A out of its resting spot. Then B' attacked C, and the resulting fight was indecisive. A short while later the newcomer attacked D, and another vicious fight ensued, with neither able to overcome the other. After 19 minutes, the newcomer had taken over A's territory and was on an equal footing with C and D. In the next 25 minutes, B' alternately fought with C and then with D, always holding its own, and between fights it drove A as often as the others did. After a total of 35 minutes of observation, B' was firmly established on A's territory, and because of B's belligerence D was displaced from its resting area, moving over to the adjacent corner. This situation still existed 24 hours later.

In this case the newcomer was very aggressive from the start and succeeded in

withstanding the attacks of the two territory-holders. By ousting the weakened A, it gained a territory and was even able to extend it at the expense of D. Here the introduction of a new fish resulted in a marked deterioration of the position of A, but the same event in Group 28 brought about an improvement for a fish in a similar situation. The critical difference was the relative aggressiveness of the two newcomers, in proportion to that of the residents.

FACTORS INFLUENCING THE ESTABLISHMENT OF TERRITORY

When the space for territories is limited, adjacent individuals may divide this space unequally but still remain in balance at the boundaries. Aggressiveness diminishes with distance from the territorial center, and this phenomenon may explain, in part, the paradox of social equals in possession of disparate areas.

Territorial balance may be achieved at the first fighting encounter or shortly afterward. If established later, within a hierarchy, the territories are taken in order of rank and result from a rise in status of the highest-ranking subordinate to equality with the despot. In such cases, prior conditioning to an area may be involved in rise in dominance level. Another distinct possibility is that the tyrant may withdraw from a portion of its range, perhaps becoming in time less aggressive, and this may enable the second-ranking individual to establish a territory.

The factors which determine whether two animals will enter upon a territorial relation are those that decide their relative aggressiveness. The larger will usually dominate; this has been repeatedly observed. Sex may be critical, since males dominate females, but not necessarily decisive. All other matters, such as

health, strength, or previous experience—in fact, all the factors involved in dominance (Allee, 1945)—are also important in the establishment of territory. The aggressiveness of each animal is the result of the complex interactions of these factors, and, since territory is a balance, variations on each side are significant for the territorial relationship.

In fifteen of the seventeen cases of territory observed in Experiments I–V, sex was determined at autopsy; the ratio was thirty-three males to twenty-seven females. Twenty-one of the males and fifteen of the females held territory, and this was roughly in the same proportion as the relative frequency of the sexes in the total population. Seven of the fifteen females that held territory were the largest in their groups, whereas only two of the twenty-one males were the largest. This suggests that size was a more important factor for females than for males. That females of heterosexual groups held territory at all is evidence that sex alone is not decisive in this kind of dominance.

In five groups there was, at first, a hierarchy with a female as alpha. In each case the next-ranking fish was a smaller male that subsequently rose to equality with the female, and the two established territories. The rise in rank of the beta fish may have been correlated with maleness; but the female alpha fish, by virtue of its experience as alpha, may have retained sufficient advantage to prevent its complete overthrow. Conversely, in three cases, second-ranking females that were the largest in their groups rose to equality with the smaller alpha males but did not overthrow them and, instead, established territories. These cases point to the importance of previous experience in relation to territory.

There were two cases in which a smaller female initially held territory alongside

two males but was ousted from her position and became omega. But in the majority of cases, territories held by males or females were stable.

Further evidence is derived from the twenty groups observed between August 5 and September 6, 1946, in connection with an experiment to be described below. Analysis of the data from these groups, which had a sex ratio of exactly 50:50, supports the points already made. Twenty-four males and eighteen females held territory; ten of the eighteen females and only seven of the twenty-four males were the largest in their groups. The relations between territoriality and sex or size held as a rule; the exceptions were due to undetermined factors.

Certain external influences modify territorialism; some of these are the configuration, subdivision, and amount of available space and the numbers of fishes present. A corollary is the factor of size; an area may be crowded for two large fishes but adequate for four much smaller ones. Preliminary experiments have been carried out with special attention to the factor of spatial subdivision.

With size of aquarium and number and size of fishes held constant, a wire-screen partition (with a 2-inch square gate at one corner) was introduced into the aquaria to divide them into adjoining compartments; in a series of twenty-seven experiments, the partition was placed about one-third of the way to one side. Twenty of the twenty-seven groups developed territories, and nineteen of them established two territories, in conformity with the arrangement of the aquarium. This is a considerably higher ratio than prevailed in Experiments I–V, with undivided aquaria. Since the groups in partitioned aquaria were maintained under somewhat different conditions of light and temperature (in a greenhouse, under natural illumination),

another set of experiments was performed, this time under the same conditions as in Experiments I-V. Two series were arranged, each consisting of ten aquaria with a partition set exactly in the middle, and alternating with these were ten control aquaria without the partitions. The first series was observed from August 5 to August 10, until stable relations had apparently been established; the second series was observed from August 29 to September 6. Table 12 presents the data with regard to types of social organization established. Fifteen of twenty groups in partitioned aquaria developed territories while only five of twenty control groups established territories.

The principal effect of the partitions was in relation to defense of boundaries. The gate became the site of interaction between the most aggressive of the fishes, alpha and beta occupying separate compartments, and the subdivision into territories appeared to be facilitated.

When the partition was set one-third of the way across the aquarium, the aggressiveness of the two territory-holders may have been correlated with amount of space. Frequently, the fish dominant in the large section kept all the others from entering it. In these cases the smaller compartment contained a typical hierarchy. Whenever the territory-holding fish in the smaller area drove a subordinate through the gate, it was promptly chased back again. After a time, movements tended to become stereotyped; the subordinate was driven with regularity and usually retired to a neutral position; but when it was evicted through the gate, the other territory-holder would be ready and waiting to drive it back. Each fish of the group played its role smoothly, and there seemed to be little friction; after a time the two territorial individuals seldom challenged each other and even

came to rest close together on opposite sides of the gate.

Not all territorial relations remained so stable; occasionally the more aggressive individual became bolder and trespassed upon the territory of the other, at first entering a short distance to drive a subordinate; the two dominant animals threatened each other, and the intruder then retreated. In several cases the more aggressive fish also began to drive its neighbor and by stages reduced the

TABLE 12

EFFECT OF SUBDIVIDING THE AQUARIA WITH PARTITION AND GATE UPON TYPE OF SOCIAL ORGANIZATION IN GROUPS OF 4 SUNFISH

SERIES	HIER- ARCHIES	TERRITORIES	
		Two	Three
1 { Experimental	3	6	1
{ Control	7	2	1
2 { Experimental	2	8	0
{ Control	8	2	0

latter's territory to a partial one. The despot kept one compartment clear for itself, but also entered the other compartment and attacked all the others. The subordinates could seldom be driven from the smaller space, because there they were relatively safer than in the larger space.

In the majority of cases the groups were first organized as hierarchies and then changed to territories after the second-ranking fish had become equal in status and dominant in one of the compartments. The second in rank resisted attack more and more vigorously, especially at the gate, upon entrance of the dominant fish, and soon the latter challenged only at the boundary. Usually the individual resident in the smaller space thus gained a territory, but occasionally

it was the other way around. That is, in some cases a fish kept the smaller space as its residence area but invaded the larger space to drive all the others. Then the second-ranking fish would progressively limit these invasions by challenges and fighting, until there existed two territories.

Essentially the same relationships prevailed in aquaria divided into two equal compartments. Here, too, it was evident that the more aggressive fish stayed alone in its compartment but often made

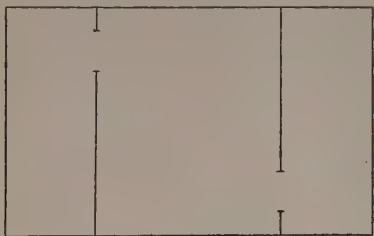


FIG. 7.—Wire-screen partitions divide aquarium into three compartments. Aquarium measures $16 \times 10 \times 10$ inches.

minor forays into the adjacent area. There was an interesting difference in orientation of the territories; the control groups generally held territories dividing a front from a rear area, but the groups in experimental aquaria followed the left-right division provided by the partition.

At the end of this series of experiments each group was observed for 15 minutes, the partition was gently raised, and observations were taken for another 15 minutes. In a typical case, one of the two territory-holders (C) had kept its side clear of subordinates and, in consequence, had very little to do to maintain its area. It drove only four times (during the first observation period), as contrasted with the activity of its neighbor (B), which drove the two lower-ranking fishes forty-six times. After removal of

the partition, C became very active and was able to drive the subordinates, since it now could reach them without trespassing at the door. C drove seventy-six times, and B drove sixty-six times; altogether, the total number of drives within the group rose from sixty-six to one hundred and fifty-seven in equal 15-minute periods of observation. At the same time, tension between B and C increased, as shown by eight challenges and eight drives between the two, as against none before. The territories were not abolished, but C proved itself to be more aggressive, continuing to keep its area free from subordinates, yet repeatedly invading B's area to drive them. The group returned to normal within a few minutes after the partition had been replaced.

Removal of the partitions in no case disrupted the territories, but there generally was an increase in challenging and driving between the territorial fishes. In four of the six groups there also followed an increased driving of subordinates by the two territory-holders. Other minor changes in status were observed; on replacing the partitions, the relations within the groups returned to normal.

The success of this method of influencing territoriality with partitions led to some preliminary trials with more complicated systems. In a set of larger aquaria ($16 \times 10 \times 10$ inches) two wire screens were introduced to provide three areas, the middle one being the largest (Fig. 7). Sixteen groups of four were observed in such aquaria; fourteen of them developed territories, an equal number being two- and three-territory situations. Hence it appears that provision of three compartments and more space resulted in establishment of a larger number of territories.

When there are three territories, the omega fish is at a decided disadvantage and may not survive, being shunted from

place to place and kept continually on the move. In one typical instance, it was seen to rest only when it retreated to a corner of the middle compartment, at the rear, and buried its head between the screen and the glass, facing away from its tormentor. Even there, it was sought out after a while and driven by all three territory-holders. The death or removal of the omega did not disrupt the territories, but subtle changes indicating an increase in tension could be noted. The fish threatened each other more often, and invasions increased in frequency. As in previous observations, the omega appeared to act as a buffer or releaser of tension between the territory-holding fishes.

There were interesting variations in the pattern of territorial division of space. Sometimes an aggressive individual took for itself two adjacent compartments and kept the others in the third. Here both a territory and hierarchy of three existed, as described for the two-compartment aquaria. In other instances the territorial fish remained in the side sections and the subordinates stayed in the middle one. The territory-holders would take turns entering the middle space to drive or would enter simultaneously while ignoring each other; in such cases individual recognition was obvious, for they often came to rest side by side, only to dart at another fish.

Another type of arrangement of partitions is shown in Figure 8. Only four groups were observed in these aquaria. In two cases, one fish held adjacent compartments, and two other fishes each held one area; the remaining fish was thus an omega. In another case one fish was so aggressive that it excluded all the others from three compartments, while a second fish maintained a territory in the fourth compartment. The fourth group was a hierarchy, with two fishes

holding partial territories, subject to invasion by the dominant individual.

As shown in Figure 9, partitions may also be arranged so that four triangular niches open into a central square. Two groups of four fishes each, when placed in such an environment, established three and four territories. The fishes stayed in the outer niches, entering the central space either to threaten a neighbor or to drive the omega, in the case of the triple-territory situation.

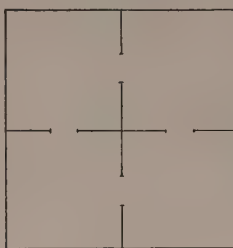


FIG. 8

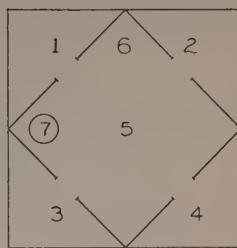


FIG. 9

FIG. 8.—Arrangement of wire-screen partitions to provide four communicating chambers. Square aquarium measures $10 \times 10 \times 12$ inches.

FIG. 9.—Arrangement of wire-screen partitions with gates to provide multiple niches as a stimulus to territory. Square aquarium measures $10 \times 10 \times 12$ inches.

Three trials were made with groups of seven fishes in such aquaria. The first trial yielded the most interesting example of territoriality so far recorded. Each corner was occupied by one individual, while a fifth was able to maintain itself in the middle section and resist the threats of the other four. A sixth fish held a partial territory within the angle made by two partitions (Fig. 9) but was subordinate to No. 5, as well as to the four that held corner territories.

The seventh fish (encircled) was omega and moved around the aquarium, driven from all directions. At the end of 3 days, the position of No. 5 had become untenable, and only the four residents in the side compartments still held territory. The three fishes in the center were

driven by these but still maintained a hierarchy. The group was almost constantly in motion; the territory-holders threatened each other, but it was obvious that they were inviolate in their own corners. First one and then another was the most aggressive in the central chamber and entered it farthest. Each fish appeared to be able to distinguish between a territorial and a nonterritorial fish, as well as perhaps individuals themselves, and drove the subordinates unerringly. Here, too, the impression was gained that the presence of subordinates

TABLE 13

EFFECT OF SPACE ON TYPE OF SOCIAL ORGANIZATION IN GROUPS OF 4 SUNFISH

Size of Aquaria (In Inches)	Territories	Hierarchies	Total Drives
4.5 × 4.5 × 4.5.....	2	8	2,864
16 × 10 × 10.....	6	4	3,560
24 × 24 × 16.....	3	5	657

lessened tension and diverted the attention of the territory-holders from each other. The group was under daily observation from August 27 through September 3, 1944, and less constantly through the rest of September; no essential change was observed.

Two other groups of seven under the same conditions established only three territories per group. In both cases an aggressive individual held two adjacent corners, while two other fishes each held one corner; none of the remaining fishes held territory.

Although these experiments with more complex arrangements of niches are preliminary, they indicate that the condition of the physical environment with regard to subdivision into niches helps determine the location and extent of territories.

The amount of space available to a

group is probably a factor in determining whether territories will be established, as shown by Shoemaker's (1939) study with canaries. A preliminary test of this factor in the sunfish was carried out from September 9 through September 29, 1945. From a stock that had been kept in the greenhouse for several weeks in extra-large aquaria (8 × 2 × 1.4 feet), twenty-eight groups (of four each) were selected, composed of fishes that were all about the same size. Ten groups were placed in 1-liter jars, ten others in medium-sized aquaria, and eight groups in much larger aquaria. Six rounds of fifteen minutes each were made between September 12 and September 29. Table 13 gives the total number of territories, hierarchies, and drives recorded under each of the three space conditions. In the matter of drives, there is a suggestion of an optimum space for the greatest number of reactions. Similarly, with regard to territory, the jars were decidedly too small, and the intermediate-sized space seemingly was most effective. These results suggest that for a given size of fish, there may be an optimum aquarium space for territoriality and/or frequency of aggressive interactions.

The effect of numbers present per unit of space has been investigated by Hixson (1946). Miss Hixson found an increase of frequency of territories in correlation with size of population, in the same volume of water. In eight groups of two fishes each, no territories were seen; in each of five groups of three, a single territory could be detected; in each of four groups of four, two territories were recorded; in three groups of six fish, two became organized as four territories, the other two as three territories; one of two groups of eight fish developed six territories, while the other developed five territories. This surprising correlation needs further study.

DISCUSSION

The literature on sunfish courtship and nesting behavior has been summarized in excellent fashion by Breder (1936). He finds that the species that have been studied are confined to a similar type of habitat and display essentially the same reproductive methods. *Lepomis cyanellus* has not been studied in the field, but in our laboratory its mating behavior followed closely the family pattern. An oval nest was constructed by the males and guarded both before and after eggs were laid, while the females participated only in egg-laying. As shown in Figure 1, all the nests were behind some opaque barrier. This closely resembles the nesting of *L. auritus* in a flowing stream, as reported by Breder (1936). Since no current existed in the aquaria, one must ascribe the position of the green sunfish nests to some other factor, possibly orientation to direct window lighting. The males entered the nests so that their heads pointed toward the angle made by the aquarium glass and the barrier, and they made sweeping movements with their tails to clear out an oval nest.

Reighard's (1902) brief discussion of the sunfish fighting pattern mentions the spreading of the gill-covers and the role of color display as an aid in driving away intruders, as well as perhaps in attracting the female. Sex differences in pigmentation and their significance in courtship were analyzed by Noble (1934) with *L. gibbosus* and by Breder (1936), with *L. auritus*. Although agreeing on the details of behavior, the authors differed with regard to the functions of male display in Darwinian sexual selection. Noble maintained that a "true" sexual selection exists in sunfish, based on the conspicuous colors of the males, which attract the attention of the females. Breder and Coates (1935) object to this hypothesis on the grounds that the sex

ratio in sunfish is nearly equal and that hence such selection would be of no practical effect. Laboratory studies by Noble and Curtis (1939) with jewel fish seem to confirm the existence of a selection mechanism in which the color display of the males attracts the females. Greenberg and Noble (1944), experimenting with the lizard *Anolis*, also support the Darwinian hypothesis in modified form. A. E. Emerson suggests that natural selection acts not upon the individual male but upon the mating pair as a unit; the brilliant male display functions to integrate the pair more effectively. However, the Darwinian concept is concerned rather with which one of several competing males enters into the mating relation.

Adult male centrarchids have long been known to hold territories during the breeding season. Abbott (1894) observed that sunfish nests are often in a row or cluster: "The occupants of the several nests do not molest each other, and never intrude beyond the limits of their own 'homes.'" Lydell (1902) recorded the fact that male black bass, preparing to nest, fight actively; in a clear artificial pond an aggressive male will prevent any other bass from building a nest within 25-30 feet. However, nests of the small-mouth bass in the "natural water" were frequently built against a stone or log so as to be shielded on one side and no farther apart than 4 feet. Lydell constructed rectangular nest frames, placed them in spaced rows, and thereby increased the number of effective breeders. This method has become standard practice in bass culture (Langlois, 1936); it utilizes one factor in determining size of territory—the physical complexity or subdivision of an area.

Much of the literature on territorial behavior of fishes has been reviewed by Noble (1938). Defense of nesting site is common among oviparous fishes. That

territorial organization may not necessarily be associated with nesting is indicated by the observations of Meyer-Holzapfel (1941). She studied eleven South American Characinidae (*Hemigrammus caudovittatus*) of unknown sex in a large aquarium ($9 \times 24.4 \times 10$ inches). The specimens averaged 7 cm. in length, presumably being adults. All except four established tri-dimensional territories; the four subordinates were relegated to "neutral areas," not defended by the other fishes. Contrary to Wunder (1930) and Breder (1936), who have found territoriality only during the mating season and held only by males, Meyer-Holzapfel suggests that there might have been a female among her territorial fishes and that they do not build nests. She concludes that territory is much more fundamental than hitherto thought.

It may be objected that, inasmuch as there were some fishes that did not have a territory, these may have been females. However, the present set of experiments with immature green sunfish of known sex supports her conclusions. Territoriality in the sunfish is independent of overt sex behavior or the genetic sex of immature individuals, although sex is a factor in deciding dominance or territorial relations in a contact-pair.

The factors influencing establishment of territory have already been discussed in part (p. 289). Underlying the behavior of adjacent territory-holders is a psychological balance at boundary lines, which manifests itself, in the sunfish, in the form of challenges or even nips but without any change in status. Although the fish must be equal at the boundaries, their territories may be decidedly unequal in extent, and this can be used as a measure of relative aggressiveness. Meyer-Holzapfel (1941) found that size of individuals was not important (within

limits of $\frac{1}{2}$ –1 cm.), in the observed social organization of *Hemigrammus*. The sunfish seem to be more sensitive to size differences, but a minor disparity in size can be overruled by other elements of a complex combination of factors. These factors are the same whether the relation is territorial or hierarchical, except for additional influences, such as the effect of residence in an area, which may reinforce the dominance drive of one or both individuals.

The hierarchy had not been investigated in any centrarchid; in fact, for teleosts generally, published accounts of hierarchies are limited to partial summarizing statements by Noble (1939a, b), two abstracts by Noble and Borne (1938, 1940), and the investigation by Braddock (1945) of a viviparous poecilid. There is substantial disagreement between Noble and Braddock, although the species involved, *Xiphophorus helleri* and *Platypoecilus maculatus*, may be interbred in the laboratory. The most important discrepancy concerns the stability of hierarchies; Noble stated that rank orders could remain unchanged for several weeks, whereas Braddock's published results show the average duration of a hierarchy of four members to be little more than a day. Although both authors claimed that the organization of their species was of the same nature as the "peck-right" society of chickens, Noble's data have not been published in full and an examination of Braddock's (1945) tables leaves the decided impression that "peck-dominance" would better describe the shifting hierarchies of *Platypoecilus*.

The social hierarchy of the green sunfish is not so stable as that of chickens. Nevertheless, my findings agree with those of Noble and Borne; some hierarchies lasted without change for more than 3 weeks, and the majority of con-

tact pair relations were stable (Table 5). The frequency of "reverse drives," i.e., the subordinate, in turn, driving its superior, was generally low; in ninety-nine of one hundred and fifty-six contact-pairs, representing twenty-six full hierarchies, not more than two return drives were recorded during the entire period of observation (Table 4). Such one-sided dominance can be called the relatively absolute, or "peck-right," type, but there were frequently instances among the lower ranks in which subordinates returned a large number of drives. This condition of instability may arise from partial or incipient territory, the "confusion" effect (p. 279), unsettled dominance early in group formation, interference by the despot in the settling of dominance between the subordinates, and other irregularities. "Peck-dominance" in fishes may straighten out in time to "peck-right," as seen in Experiment VI; but, even after a long period, pair-contacts may still be indecisive.

In all but two of the one hundred and seventy-two groups that I observed, there was at least one subordinate individual; thus, where territory was held, hierarchal relations also existed, and the fishes defending areas drove the subordinates but not one another. Even in the groups organized solely as hierarchies, the drive to hold territory could be detected in the form of the partial territories held by one or more of the subordinates. Such semi-territories were seen in seventeen of the twenty-seven hierarchy groups of Experiments I-V.

These facts indicate that the principles of hierarchy and territory are not sharply separate but interplay in a variety of ways to shape the form of sunfish organization. It is highly probable that hierarchal relations of some sort exist in every instance of territory, but there is reason to believe that certain species that

exhibit hierarchy are not at all territorial (Braddock, 1945). Whether territoriality is entirely absent even in these cases, or perhaps can be detected in modified form, needs to be further investigated.

A simple form of leadership can be discerned in groups of sunfish. It expresses itself in facilitation of various forms of behavior, especially feeding and the driving of subordinates. Leadership implies initiative and control of the pace of an activity, usually by one individual or alternately by several. A test for its presence in the sunfish was made by putting six groups through a learning situation to determine whether the most dominant individual in a group is also the leader. It was impracticable to secure the learning time for each individual; the six dominant fishes "led" in 47 per cent of the total trials (60), whereas the chance expectation is approximately one-half of this. Also a comparison of the average group performance with the learning shown by isolated sunfish (Fig. 3) indicates that there was a marked facilitation of learning in the groups.

Welty (1934) demonstrated that grouped goldfish are markedly superior to isolated ones in similar learning tests. It is possible to ascribe part of the group advantage to leadership, but it was observed also that isolated sunfish are more easily startled and become conditioned against elements of the test situation. Thus several isolated fishes gave erratic learning performances, while others did almost as well as the groups. The elimination of such variations may be part of the group benefit.

The tendency of the dominant fish to be the leader has far-reaching implications for further study. Settled hierarchies in chickens have greater survival value than groups kept constantly in reorganization (Guhl and Allee, 1944). If the dominant individual were also the

leader, it could contribute to group survival; this would balance some of the destructive individual advantages of aggressive drive.

The outstanding group value of aggressiveness in the sunfish probably centers about the importance of territory-holding in egg-laying, and the defense of eggs and young by the males. Fishes strung out along the shore on individual nests constitute questionable groups, but from an ecological point of view they are part of an integrated breeding aggregation. Territoriality spaces the nests and may make for more effective breeding.

The role of hierarchy in breeding survival is less obvious. A clue is afforded by the observations centering about the omega individual in a territorial situation. When three members of a group defend areas, the fourth almost always is severely punished, being driven at an excessive rate and often killed. Removal or death of the omega was followed by a rise in tension and increased frequency of aggressive contact among the territory-holders. Introduction of a newcomer centered attention upon it and reduced other aspects of intra-group friction. Thus it appears that these subordinates have a definite function in integrating the group.

SUMMARY

Groups of four immature sunfish (*L. cyanellus*), observed for periods of 19-25 days in small bare aquaria, maintain hierarchies or territories or both. Hierarchies are fairly stable and become progressive-

ly more so with time. Males usually dominate females, and the larger individuals tend to dominate smaller ones.

Among these fishes, hierarchy represents distinct levels of aggressiveness, whereas territoriality arises from a balance between almost equally aggressive individuals. This balance may be struck at first encounter; but, when it occurs later within a hierarchy, territories are first established by the two highest-ranking individuals, then by the third, and, rarely, by the lowest. Seventeen of forty-four groups kept in bare aquaria developed territoriality. In twelve cases, three of the four fishes held territories, while the fourth was subordinate to all. In one group each member held territory; here few aggressive contacts were observed.

Subordinates frequently defended areas against all but the most dominant fish. This "partial" territory seems intermediate between hierarchy and territory.

Groups tested in a simple maze-learning situation were superior to isolated controls. Leadership through the maze shifted at almost every trial, but the dominant individual tended also to be the "leader."

Aquaria divided into compartments by means of wire-screen partitions with square gates favored formation of territories, in direct proportion to the complexity of the subdivision.

Subordinates appear to lessen tension among territory-holding fishes; removal of the omega from aquaria with three territories markedly increased aggressive activity among those remaining, whereas the introduction of a new fish led to their attacking it instead of one another.

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